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Population Regulation in Eastern Canadian Atlantic salmon (*Salmo salar*) populations

Régulation des populations de saumon atlantique (*Salmo salar*) de l'est du Canada

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FOREWORD

This document is a product from a workshop that was not conducted under the Department of Fisheries and Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It is one of a number of contributions first tabled at a DFO-SARCEP (Species at Risk Committee / *Comité sur les espèces en péril*) sponsored workshop in Moncton (February 2006) to begin the development of a 'Conservation Status Report' (CSR) for Atlantic salmon. When completed in 2007, the CSR could form the basis for a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report, recovery potential assessment and recovery strategy, and most importantly, enable DFO to implement pre-emptive management measures prior to engagement in any listing process.

AVANT-PROPOS

Le présent document est issu d'un atelier qui ne faisait pas partie du processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Il fait partie des nombreuses contributions présentées au départ lors d'un atelier parrainé par le MPO-SARCEP (*Species at Risk Committee* / Comité sur les espèces en péril) à Moncton (février 2006) en vue de commencer l'élaboration d'un rapport sur la situation de la conservation du saumon atlantique. Lorsqu'il sera terminé, en 2007, ce rapport pourrait servir de base à un rapport de situation du Comité sur la situation des espèces en péril au Canada (COSEPAC), à une évaluation du potentiel de rétablissement et à un programme de rétablissement mais, avant tout, il permettra au MPO de mettre en œuvre des mesures de gestion anticipées avant même de s'engager dans un processus d'inscription.

Abstract

The timing and nature of density-dependent survival in Atlantic salmon populations was analysed using electrofishing data from nine populations in the Maritime Provinces to evaluate its role in freshwater environments, and smolt-to-adult return-rate data from 15 populations in eastern Canada to evaluate its importance in marine habitat. Three spawner-recruit models, a Beverton-Holt, a Ricker and a one-parameter density-independent model, were fit to each data series using maximum likelihood, and model fits were compared using likelihood ratio tests. Within fresh water, no single, unequivocal pattern was evident with respect to the timing of density dependence. Of the six egg-to-age-0 transitions, the addition of a second parameter for density dependence resulted in a statistically better fit in three cases. In six of the nine age-0-to-age-1 transitions, the addition of second parameter provided a statistically better fit, as was also the case in three of the nine age-1-to-age-2 comparisons. Of the nine populations, density dependence was not detected in two populations, was detected in only one transition in two populations, detected in two transitions in four populations and was detected in all three transitions in the remaining population. Overcompensation was not detected in these data. The Ricker model (which exhibits overcompensation) did not provide a statistically significantly better fit in any of the 25 comparisons, and when comparisons were made over all populations, the Beverton-Holt model (which does not exhibit overcompensation) provided a statistically better fit for the three age class transitions investigated here. In the marine environment, density dependence was potentially detected in three of the 15 return-rate data series for salmon maturing after one winter at sea, but was not detected in any of the nine return-rate data series for fish maturing after two winters at sea. Carrying capacity for age-1 salmon was found to be highly variable among populations. Using a mixed-effects model, the median carrying capacity was estimated to be 24.8 parr/100m^2 with 95% of the probability density falling between 3.8 and 165.9 parr/100m^2. The variability in both the timing of density dependence and carrying capacity for parr highlights the need for population-specific data for establishing reference points or when planning recovery or enhancement activities.

Résumé

Nous avons analysé les paramètres temporels et la nature de la survie dépendante de la densité chez les populations de saumon atlantique à l'aide de données provenant de l'électropêche menée sur neuf populations des provinces maritimes afin d'évaluer le rôle de cette espèce dans les environnements d'eau douce. Nous nous sommes également servis de données sur les taux de remonte saumoneaux-adultes de 15 populations de l'est du Canada pour évaluer l'importance de ce poisson dans l'habitat marin. Nous avons ajusté trois modèles géniteurs-recrues (modèle de Beverton-Holt, modèle de Ricker et modèle à un paramètre indépendant de la densité) à chaque série de données selon le maximum de vraisemblance, et nous avons ensuite comparé les ajustements des modèles au moyen de tests du ratio de vraisemblance. En eau douce, aucun profil univoque n'est ressorti en ce qui concerne les paramètres temporels de la dépendance à la densité. Dans trois des six transitions œuf-âge 0, l'ajout d'un deuxième paramètre pour la dépendance à la densité a résulté en un meilleur ajustement sur le plan statistique. Dans six des neuf transitions âge 0-âge 1, l'ajout d'un deuxième paramètre a également donné un meilleur ajustement sur le plan statistique, de même que dans trois des neuf comparaisons entre l'âge 1 et l'âge 2. Parmi les des neuf populations, nous n'avons relevé aucune dépendance à la densité chez deux populations, une dépendance à la densité dans une transition uniquement chez deux populations, dans deux transitions chez quatre populations et une dépendance à la densité dans chacune des trois transitions chez la les autres populations. Nous n'avons relevé aucune surcompensation dans ces données. Le modèle de Ricker (qui montre la surcompensation) n'a pas donné un ajustement vraiment meilleur sur le plan statistique dans aucune des 25 comparaisons, et lorsque nous avons comparé toutes les populations, le modèle de Beverton-Holt (qui ne montre pas la surcompensation) a donné un meilleur ajustement sur le plan statistique pour les trois transitions des classes d'âge présentement étudiées. En milieu marin, nous avons probablement relevé une dépendance à la densité dans trois des 15 séries de données sur les taux de remonte des saumons arrivant à maturité après un hiver en mer, mais nous n'avons pas relevé de dépendance à la densité dans aucune des neuf séries de données sur les taux de remonte des poissons arrivant à maturité après deux hivers en mer. La capacité biotique du saumon d'âge 1 s'est révélée grandement variable d'une population à l'autre. À l'aide d'un modèle à effets mixtes, nous avons estimé que la capacité biotique moyenne est de 24,8 tacons/100m2, alors que 95 % de la densité de probabilité descend entre 3,8 et 165,9 tacons/100m2. La variabilité des paramètres temporels de la dépendance à la densité et de la capacité biotique des tacons démontre bien que nous devons recueillir des données propres aux populations pour établir des points de référence ou planifier des activités de rétablissement ou de mise en valeur.

Introduction

The status of Atlantic salmon populations in the Atlantic Provinces varies regionally. Populations around the Bay of Fundy and Nova Scotia's Atlantic coast are in strong decline, whereas the status of Nova Scotia and New Brunswick Gulf of St. Lawrence populations range from declining to stable (DFO 2003, Gibson and Hubley 2006). In Newfoundland and Labrador, some populations are increasing, whereas others are decreasing or stable (Dempson et al. 2006, DFO 2005, Gibson and Hubley 2006). Atlantic salmon populations have a rich, complex life history that is highly variable (Hutchings and Jones 1998). Variability and plasticity in life history characteristics, such as size and growth in fresh water, biological characteristics of smolts, size and growth in marine water, survival in fresh water and at sea, and fecundity for eastern Canadian populations is summarised by O'Connell et al. (2006). The timing and nature of population regulation in juvenile salmon populations in Atlantic Canada may be correspondingly variable; a hypothesis investigated using meta-analysis in this document.

The concept of population regulation is closely tied to the concept of population persistence. Although population size may fluctuate widely through time, long-term persistence and a tendency not to grow unchecked implies a regulatory mechanism that controls population size (Royama 1992). Such regulation may be density-independent or density-dependent, termed fragile and robust regulation by Royama (1992). While it's possible for populations to persist without exhibiting continual growth in the absence of density dependence, it is extremely unlikely. Under these conditions, population size over time should behave as a random walk, a behavior that is inconsistent with the concepts of persistence and a bound on population size. So, while density-independent factors can markedly influence population size, questions about the timing and nature of population regulation are really questions about the timing and nature of density dependence within the population. Here, we focus on density-dependent survival, although density dependence can influence other life history characteristics such as growth and fecundity.

The nature of population regulation in salmonids is of more than theoretical interest. The question of when and how year class size is determined is a fundamental question in fisheries biology that spans a time period of nearly 100 years (e.g. Hjort 1914, Myers and Cadigan 1993), the answer to which has implications for many questions in fisheries management, including the effects of fishing on abundance, as well as being a key determinant of the effectiveness of stocking. It is also important for the development of models used for setting biological reference points (Clark 1991), determining the limits of exploitation (Myers and Mertz 1998a), and for evaluating the potential benefits of recovery activities for at-risk populations (Trzcinski et al. 2004).

In the context of population regulation, compensatory density dependence (where the rate of population increase is negatively correlated with population size) is implied. When compensatory density dependence occurs over the full range of population sizes, survival between life stages is a decreasing monotonic function of the population size such that the maximum survival rate occurs at a population just greater than zero. An alternative scenario, an abundance threshold below which survival switches to an increasing

function of population size, is also possible and is termed depensation (Clark 1976). However, due to its de-stabilizing characteristics, it is not a regulatory mechanism (Rose et al. 2001).

The concept of depensation, which occurs at low abundance, is controversial in fish population biology, with most information coming from spawner-recruitment (SR) analyses. Myers et al. (1995b) did not find evidence of depensation in 125 of 128 spawner-recruit time series they examined. Liermann and Hilborn (1997) conducted a similar analysis with a different depensatory model and concluded that depensation may be more common that suggested by Myers et al. (1995b). Barrowman et al. (2003) did not find evidence of depensation for coho salmon, a similar result to Gibson and Myers (2003) for alewife. Both authors found that most SR data sets are not informative about the shape of the SR function at the origin. However, there is empirical evidence that depensation may exist based on population recovery. Populations that undergo large declines often do not rapidly recover (Hutchings 2000, Hutchings 2001), potentially indicating that depensatory population dynamics may be quite common.

There is also uncertainty about the shape of the SR curve at high abundance, but typically one of two options is used (Hilborn and Walters 1992). The first is the Beverton-Holt model, which is based on the assumption that competition within a cohort results in a mortality rate that is a linear function of the number of fish alive in the cohort at any time. The result is an SR curve that behaves asymptotically: recruitment increases as spawner abundance increases, albeit very gradually at high abundance. The other model is the Ricker model, which is based on the assumption that the mortality rate is dependent on the initial cohort size. Based on this assumption, increasing spawner abundance leads to increases in recruitment up to a maximum, after which further increases in spawner abundance have the effect of reducing the number of recruits. This phenomenon is known as overcompensation. Solomon (1985) reviewed the evidence for both dome-shaped and asymptotic curves for Atlantic salmon, and concluded that asymptotic curves were most appropriate. However, as acknowledged by the author, the possibility exists that many of the populations were at low enough levels that a descending right-hand limb might not be detectable.

While several other SR functions have been proposed, one that warrants mention for salmonids is the hockey-stick model (Barrowman and Myers 2000). This model is based on the concept of territoriality: some finite number of territories are available to a population. As abundance increases, survival is density-independent until all territories are filled, after which it is density-dependent.

Rose et al. (2001) provide a detailed review of compensation in fish populations. They suggest that density-dependent mortality can be caused by density-dependent responses by predators or via density-dependent growth, reproduction or movement affecting survival, and summarize considerable evidence for each case. The concept of density-dependent mortality is thus closely tied to that of carrying capacity and resource limitation (Beverton 1995). For diadromous species such as Atlantic salmon, the potential mechanisms for density-dependent mortality likely vary with environments. In

fresh water, resource limitation (bottom-up control) may lead to density-dependent mortality, as implicated when growth rates are also density dependent. In the marine environment, resources are likely less limiting as fish are less concentrated, but density-dependent predation (top-down control) is a plausible mechanism. Density-dependent mortality as result of predation may occur as either a numerical (increase in the number of predators) or functional (behavioral responses that change predation rates) response to the prey density (Begon et al. 1990). In the case of salmon, it is unlikely that overall predator abundance increases on the relatively short time period that salmon remain in a particular environment. However, predators may aggregate in response to increased salmon abundance, a functional response similar to that suggested for predators foraging on reef fish (Hixon 1998).

There is considerable evidence for density dependence in the juvenile Atlantic salmon life stages in fresh water, although in some studies, such as those in highly productive areas, it was not observed (Gibson 1993). For example, O'Connell et al. (2006) show strong evidence of density dependence between the egg and smolt life stages in Western Arm Brook, Northeast Brook, Trepassey River, and Conne River in Newfoundland. However, while there is evidence of density dependence in salmon in freshwater habitat, the mechanism is less well understood and the point at which density dependence begins to operate, its intensity and its precise form are less clear (Milner et al. 2003). Density-dependent size-at-age has been demonstrated for salmon parr (Gibson 1993, Korman et al. 1994, Amiro et al. 2003) which could lead to density-dependent survival. Armstrong and Griffiths (2001) found that the proportion of parr sheltering in an indoor stream decreased with increasing density, an observation that may have consequences for over-wintering survival as well as carrying capacity. While these studies suggest that density dependence may occur at older life stages, other studies indicate that density dependence occurs only in the very early life stages during a 'critical period' (Elliott 2001). This latter position is commonly adopted. In a recent review of population regulation in salmon and trout populations, Milner et al. (2003) conclude that density dependence in salmon is likely sustained longer than in trout and may last at least through the first summer. Thereafter, up to the smolt stage, survival has generally been found to be density independent.

In the next two sections, the nature and timing of density-dependent survival in salmon populations in eastern Canada is evaluated for freshwater habitat using electrofishing data from nine rivers in the Maritime Provinces, and for the marine environment using smolt-to-adult return rate data for fifteen populations in Eastern Canada.

Density Dependence in Fresh water

While density dependence has been shown to occur for salmon in fresh water, less information is available about the timing and nature of the density dependence. As a first step to developing a population dynamics model for inner Bay of Fundy salmon, Trzcinski et al. (2004) fit models to electrofishing data sets for two inner Bay of Fundy populations to evaluate the timing of density dependence. They compared the fits of a

density-independent model to a model with density dependence (a Beverton-Holt stock recruitment model) for three age-class transitions: egg-to-age-0, age-0-to-age-1 and age-1-to-age-2, and concluded there was only evidence of density dependence between age-0 and age-1. Here, their analysis is extended to include data from nine populations in the Maritime Provinces, in an attempt to answer the following questions:

1) When does density dependence occur in fresh water?
2) Is overcompensation characteristic of salmon populations?
3) Can density dependence be quantified from these data?

For this analysis, the annual mean density of age-0, age-1 and age-2 salmon, obtained by electrofishing, and the annual egg depositions estimated from stock assessments are used. A summary of the data series used in the analysis is provided in Table 1.

Methods

Spawner-recruit (SR) models are a widely accepted tool for analyzing population dynamics (Moussalli and Hilborn 1986, Myers et al. 1999). They provide a basis for estimating biological reference points for management (Myers and Mertz 1998b, Gibson and Myers 2004), a method for evaluating the effects of mortality caused by pollution, dams or other human activities (Barnthouse et al. 1988, Hayes et al. 1996), and are a suitable tool for investigating the timing and nature of density dependence (e.g. Myers and Cadigan 1993). Here, three SR models are fit to the egg and juvenile data from the nine rivers. The first of these models is a one-parameter model in which the number (or density) of fish of age a in year t, denoted $N_{t,a}$, is a density-independent function of the number (or density) in the preceding age class in the preceding year:

$$N_{t,a} = \alpha N_{t-1,a-1}.$$

The interpretation of α differs slightly depending on the data. When fit to the age-0-to-age-1 juvenile densities, it is the density-independent age-specific survival rate between age classes. However, due to the differences in the data reporting (eggs are reported as the estimated egg deposition in the river, whereas the age-0 data is the mean density in the river), when the model fit to the egg-to-age-0 data, α is scalar that is proportional to egg-to-age-0 survival, but differs from the actual survival by the number of effective habitat units within the river (or the ratio of the mean density of fish obtained by electrofishing to the number of fish in the population) which is unknown. Finally, when fit to the age-1-to-age-2 data, α is a composite parameter that combines both survival and probability of smoltification at age-2. In all cases, the true value of α would be between zero and one.

The other two models used here are the most commonly used two-parameter SR models: the Beverton-Holt and Ricker (Hilborn and Walters 1992). These models differ fundamentally in their assumptions of the underlying biology, the latter showing a decline in recruitment at higher spawner abundance, a phenomenon known as

overcompensation. The Beverton-Holt model gives $N_{t,a}$, as a density-dependent function of $N_{t-1,a-1}$:

$$N_{t,a} = \frac{\alpha N_{t-1,a-1}}{1 + (\alpha N_{t-1,a-1}/R_{asy})}.$$

Here, α is the slope at the origin, and in the deterministic model is the maximum survival rate between age classes in the absence of density dependence at low population sizes (Myers et al. 1999) and R_{asy} is the asymptotic recruitment level. As $N_{t-1,a-1}$ approaches infinity, R_{asy} is the limit approached by R (Beverton-Holt models are often written in terms of the half saturation constant, K, which is related to R_{asy} by: $R_{asy} = \alpha K$), and is the carrying capacity for age-a fish expressed as a density. The same caveats apply to the interpretation of α when fit to the egg-to-age-0 data.

The Ricker model also gives $N_{t,a}$, as a density-dependent function of $N_{t-1,a-1}$:

$$N_{t,a} = \alpha N_{t-1,a-1} e^{-\beta N_{t-1,a-1}}.$$

Here, the interpretation of α is the same as for the Beverton-Holt model, as written above, and β is a shape parameter that determines how rapidly survival declines as abundance increases.

Parameter estimates for each population and model were obtained using maximum likelihood assuming a lognormal error structure for recruitment (Myers et al. 1995a). Denoting the Beverton-Holt spawner-recruit function as $g(N_{t-1,a-1})$, the log-likelihood is given by:

$$\ell(\alpha, R_0, \sigma) = -n \log \sigma\sqrt{2\pi} - \sum \log N_{t,a} - \frac{1}{2\sigma^2} \sum \log\left(\frac{N_{t,a}}{g(N_{t-1,a-1})} \right)^2$$

where σ is the shape parameter for a lognormal distribution and n is the number of paired observations. We used profile likelihoods to assess the plausibility of the individual parameter estimates given the data. The log profile likelihood for α, $\ell_p(\alpha)$, is:

$$\ell_p(\alpha) = \max_{R_0 \sigma} \ell(\alpha, R_{asy}, \sigma).$$

The maximum likelihood estimate for α occurs where $\ell_p(\alpha)$ achieves its maximum value. The plausibility of other possible values of α was evaluated by comparing their log likelihoods with the maximized log likelihood. A likelihood ratio based 95% confidence interval for α was calculated as:

$$\{\alpha : 2\left[\ell_p(\alpha^{MLE}) - \ell_p(\alpha)\right] \leq \chi_1^2(0.95)\}.$$

The profile likelihood and the associated 95% confidence interval for R_{asy} were found similarly.

In isolation, many datasets are relatively uninformative about these parameters. Based on the idea that many populations of the same or similar species share similar life history strategies, Myers et al. (1999, 2001) developed methods that allow parameter estimates from several populations to be combined, providing a probability distribution for the parameter estimates at some higher organizational level such as the species. The resulting probability distributions can be combined with comparatively limited population-specific data to make inferences at the level of the specific population. This approach, known as meta-analysis, allows conclusions to be reached by drawing upon data from many populations. Hierarchical Bayesian methods (Carlin and Louis 1996) are one approach to meta-analysis that has been applied to salmon production (Prevost et al. 2001). Mixed-effects models are an alternate approach that have the advantage that a joint prior distribution for the fixed effects and variance components doesn't have to be specified. Estimates are obtained using maximum likelihood, and are identical to empirical Bayes estimates in that the priors are obtained from the data (often referred to as MLE priors). As such, these priors can then be used as priors for Bayesian analyses of population dynamics for stocks where little data exists about the stock under investigation (Myers et al. 2002).

As will be seen in the results, the strongest evidence for density dependence occurs between age-0 and age-1, with little evidence for overcompensation, although parameter estimates are not completely satisfactory. Therefore, Beverton-Holt models were also fit to the age-0-to-age-1 data using a mixed-effects model to evaluate whether more plausible parameter estimates could be obtained. The models were fit using the approximate maximum likelihood algorithm of Lindstrom and Bates (1990), using the S-Plus nonlinear mixed-effects library of Pinheiro and Bates (1999).

To simplify notation we use F (for "fry") to denote age-0 and P (for "parr") to denote age-1 juvenile salmon. We have data for several salmon populations and for each population i, we have n_i observations of the form (P_{ij}, F_{ij}), $j = 1....n_i$. These observations are modelled as:

$$P_{ij} = \frac{\alpha_i F_{ij}}{1 + \alpha_i F_{ij} / \mathrm{R}_{asyi}} e^{\varepsilon_{ij}}$$

where $\alpha_i > 0$, $\mathrm{R}_{asyi} > 0$ and $\varepsilon_{ij} \sim N(0, \sigma_i^2)$. As specified, error variance differs among populations, and errors are multiplicative. Taking the natural logarithms of both sides yields:

$$\log P_{ij} = \log(\alpha_i) + \log(F_{ij}) - \log(1 + \frac{\alpha_i F_{ij}}{\mathrm{R}_{asyi}}) + \varepsilon_{ij}.$$

We define $\log \tilde{\alpha}_i = a + b_i$ and $\log \tilde{\mathrm{R}}_{0i} = c + d_i$:

$$\log P_{ij} = a + b_i + \log(F_{ij}) - \log(1 + \left(\frac{\exp(a + b_i) F_{ij}}{\exp(c + d_i)} \right) + \varepsilon_{ij}.$$

One approach to fitting this model is to treat a, b_i, c and d_i as fixed effects, which is the equivalent to fitting to each data series individually as was done earlier in this section when evaluating the timing of density dependence. The alternative method, used here, takes advantage of similarities among populations. We assumed that $\log \alpha_i$ and $\log \mathrm{R}_{asyi}$ are normally distributed random variables and fit the model treating a and c as fixed, and b_i and d_i as random effects. Here, a and c are the means of $\log \alpha_i$ and $\log \mathrm{R}_{asyi}$ respectively, and b_i and d_i are the random deviates for each population, such that:

$$\begin{pmatrix} b_i \\ d_i \end{pmatrix} \overset{iid}{\sim} \mathrm{N}\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma^2_b & 0 \\ 0 & \sigma^2_d \end{pmatrix} \right].$$

Note that when estimated using this model, α_i and R_{asyi} are the median survival rates and carrying capacities for an age class within each population.

Results

In total, models were fit to 24 data series, including six for egg-to-age-0 transitions and nine series each for the transitions from age-0-to-age-1 and from age-1-to-age-2 (Figure 1). No single, unequivocal pattern emerges. For example, in the case of the NW Miramichi River, the slope at the origin of the Beverton-Holt model fit to the eggs-to-

age-1 data is infinite, suggesting no relationship between egg deposition and the abundance of age-0 fry. In contrast, the fit to the Tobique River egg-to-age-0 data suggests a strong relationship between these variables.

Similarly, no pattern is immediately evident for the timing of density dependence among populations. Of the six egg-to-age-0 transitions, in three cases the addition of a second parameter for density dependence resulted in a statistically better fit (Table 2). Of the nine age-0-to-age-1 transitions, in six cases the addition of second parameter provided a statistically better fit, as was also the case in three of the nine age-1-to-age-2 comparisons. Of the nine populations, density dependence was not detected in two populations, was detected in only one transition in two populations, was detected in two transitions in four populations and was detected in all three transitions in the remaining population. The two populations in which density dependence was not detected (Stewiacke River and Margaree River) had two of the highest observed age-1 densities, although the absence of density dependence suggests that carrying capacity may not have been reached for these populations. Overall, the results indicate that the timing of density dependence within fresh water is highly variable among populations.

Despite the lack of a consistent pattern in the timing of density dependence, the data are more informative about the nature of density dependence. As evidenced by the statistical comparison between the Ricker and Beverton-Holt models (Table 3), overcompensation does not appear to be characteristic of these Atlantic salmon populations. Statistically, the Ricker model did not provide a significantly better fit in any of the 25 comparisons (likelihood ratio test; 95% C.L.), whereas the fit of the Beverton-Holt model was significantly better in four of the individual comparisons. When comparisons were made over all populations combined, the Beverton-Holt model provided a statistically better fit (likelihood ratio test; 95% C.L.) for all three transitions investigated here.

One difference in the application of SR models used here from more traditional applications with marine populations (using spawning biomass and number of recruits) is that the α parameter has a direct interpretation as the maximum annual survival rate (at low population sizes in the absence of density dependence) between the stages. As such, the true value of α cannot exceed one, although in five of the Beverton-Holt age-0-to-age-1 models, and in two of the age-1-to-age-2 models, the estimate of α did exceed one (Table 2). Estimation of α requires extrapolation to the origin which can be problematic particularly when most data is at higher densities. Here, we use the mixed-effects model fit to the age-0-to-age-1 data to evaluate whether the same data series are simply uninformative about α, or whether the estimates are high for some other reason. If the data are uninformative, the estimates obtained from the mixed-effects model would be expected to be better (i.e. more plausible) than those from the models fit individually due to the influence of the data from other populations. If the estimates do not change, they would be assumed to be high for some other reason (e.g. sampling bias).

Figure 2 is a meta-analytic summary of the individual fits for each population and the mixed model results for salmon at the species level. The raindrop plots (Barrowman 2000) for each population (light grey shaded region) show the profile likelihood for each

parameter, the width of which can be used to gauge the relative plausibility of different values. When estimated for each population individually, the maximum age-0-to-age-1 survival was well determined for only two of the eight populations, the Restigouche and the SW Miramichi rivers. These populations also have the lowest estimates. Bounds for the confidence intervals could be determined for all populations, although one population, the Tobique River, has a lower bound greater than one. With all populations combined, the mixed model random effects distribution for $\log \alpha$ has a mean of -0.09 and a standard deviation of 0.476. Forty-two percent of the mass of this probability distribution is within a range that is not biologically plausible ($\alpha > 1$).

Overall, the individual datasets contained more information about the habitat carrying capacity than the maximum age-0-to-age-1 survival, although carrying capacities varied widely between populations (Figure 2). Two exceptions were the Margaree and Stewiacke populations, for which the profile likelihoods were ramped. With all populations combined, the mixed model random effects distribution for $\log R_{asy}$ has a mean of 3.21 and a standard deviation of 0.97. The median habitat carrying capacity for age-1 salmon populations is therefore 24.8 parr/100m^2, with a 95% confidence interval of 3.8 to 165.9 parr/100m^2.

Estimates of α obtained from the mixed model are similar to those from the individual fits (Figure 3, Table 4). In contrast, the estimates of R_{asy} for three populations (Margaree, Stewiacke and SW Miramichi) dropped substantially when estimated using the mixed-effects model, consistent with the wide confidence intervals obtained for R_{asy} for these populations (Figure 2).

A comparison of the age-0-to-age-1 data series is shown in Figure 4. Data are plotted on the same scale, and models from both the individual and mixed model fits are shown. Differences in the fits are subtle, although since data are plotted on the same scale, some differences are evident. First, the two populations with the greatest change in the carrying capacity estimate appear to have different issues: the Margaree populations have no data near the origin as well as little contrast in the data, whereas the Stewiacke data is all near the origin but perhaps contain too little contrast to estimate carrying capacity. The rivers with the best estimates for both parameters (Restigouche and NW and SW Miramichi) are those with the greatest range of observed densities. Finally, with the exception of the Stewiacke River, the carrying capacity for age-1 parr of the Gulf of St. Lawrence rivers (Restigouche, Margaree and NW and SW Miramichi) appears higher than that of Bay of Fundy and Nova Scotia Atlantic coast rivers.

Density Dependence in the Marine Environment

Density dependence in Atlantic salmon populations in the marine environment is relatively unstudied. Here, we apply the approach used above to the smolt-to-adult returns data from 15 populations (Table 5) to determine whether density dependence can be detected in the marine environment. Three models (density independent, Beverton-

Holt and Ricker) were fit to data for the smolt-to-1SW return data and smolt-to-2SW return data individually. As such, the statistical comparisons do not distinguish between survival rates and age-at-maturity when testing for density dependence.

Results

Of the 15 smolt-to-1SW comparisons (Figure 5), density dependence was potentially detected in three populations: Campbellton, NE Trepassey, and St. Jean. However, both the Campbellton and NE Trepassey models produced biologically impossible parameter estimates (Table 6) from the Beverton-Holt model, although not so from the Ricker. For the other 12 populations, the density-dependent models produced infinite estimates of the carrying capacity in five cases, such that the fits were virtually identical to the density-independent models, a result that strengthens conclusions about the lack of density dependence in the marine environment for these populations.

Density dependence was not detected in any of the nine smolt-to-2SW returns (Figure 6). Similar to the 1SW results, five of the nine density-dependent models produced infinite estimates of the carrying capacity (Table 7), again strong evidence against density dependence in the marine environment.

Discussion

Several interesting factors have surfaced during this analysis of the electrofishing data. First, the timing of population regulation appears variable among salmon populations, but appears most frequently between age-0 and age-1. Additionally, in some populations, it appears to take place gradually over a couple of years, and in others it appears to be relatively rapid, occurring in only one age class. This result is in contrast with the position of Milner et al. (2003), in a recent review of population regulation in salmon and trout populations, that "density-dependent mortality only operates for comparatively short periods of the life cycle, during critical stages, when regulation of population size was achieved by competition for limited resources". This position is partially based on the work of Elliot (1989, 1993a) for a brown trout population, in which density dependence took place during a critical period approximately 30 to 70 days from when fry dispersed from the spawning gravels. Additional evidence was derived from studies that have shown density dependence occurring throughout the first summer followed by density-independent survival through to the smolt stage (Gee et al. 1978, Egglishaw and Shackley 1977, Gardiner and Shackley 1991), again in contrast to the results presented herein. Armstrong et al. (2003) documents the differences in freshwater habitat requirements of salmon of different ages. If habitat requirements differ with age or size, and the availability of these habitats varies among rivers, then the timing of density dependence would also be expected to vary from population to population, consistent with our results. The results presented here are also consistent with the findings of Myers and Cadigan (1993) for Atlantic cod where density dependence can occur for 3 or more years.

The Ricker model has often been used for modeling Atlantic salmon population dynamics (e.g. Chaput et al. 1992b), but often without systematic approaches to model selection being applied prior to its use. This may have contributed to the conflicting results reported for various populations within the last 30 years. For example, Gee et al. (1978) working on an English river, proposed dome shaped curves for these populations. Buck and Hay (1984), working on a Scottish stream, did not find evidence that the number of migrating smolt decreased as egg depositions increased despite working at depositions well above Elson's norm. Jonsson et al. (1998) proposed an asymptotic model for salmon in a river in Norway. Chaput et al. (1992) fit both a Beverton-Holt model and Ricker model to data from the Margaree River and concluded that the Ricker model provided the better fit to the data. Kennedy and Crozier (1993) decided that a dome shaped curve provided a better fit to egg-to-smolt data on River Bush, but it was not clear what, if any, selection criteria were applied. Here, when taken on the whole, the Beverton-Holt model provided a better fit to the data for all age classes, and we did not find a single case where the Ricker model provided a statistically significant better fit than did the Beverton-Holt. As an alternative approach, Michielsens and McAllister (2004) advocated a Bayesian hierarchical approach to modeling salmon population dynamics which included both the Beverton-Holt and Ricker models. Posterior probability densities were developed from data for nine populations with the Beverton-Holt model providing a slightly better fit to the data.

As pointed out by Myers et al. (2001) and Gibson and Myers (2003), when the data for several populations are simply standardized and plotted on the same scale (Figure 4), patterns become evident and populations that are different are easily identified. One of the most interesting factors to come out of this analysis is the relative difference in the carrying capacity for age-1 parr between the Gulf of St. Lawrence populations and those on the Atlantic coast and Bay of Fundy. The one exception to this pattern is the high carrying capacity of the Stewiacke River population, one of the endangered inner Bay of Fundy salmon populations. The reason for these differences is unclear. Habitat in many Atlantic coast rivers has been impacted by acid rain, although pH problems are not known to be an issue for Bay of Fundy rivers.

Chadwick (1987) concluded that freshwater survival is comparatively less variable than marine survival, a result similar to that of Peterman (1981) for coho salmon, and of Jonsson et al. (1999) for a salmon population in Norway. Based on the individual analysis using the Beverton-Holt model herein, σ averaged 0.490 (std. dev. = 0.204) for egg-to-age-0 survival, 0.373 (std. dev. = 0.107) for the age-0-to-age-1 transition, and 0.488 (std. dev. = 0.206) for the age-1-to-age-2 transition. Based on the density-independent model σ for the smolt-to-1SW, returns averaged 0.383 (std. dev. = 0.148) and for the smolt-to-age-2, returns averaged 0.483 (std. dev. = 0.139). These results suggest that the variability in survival in freshwater is not less than that in the marine environment. Although density dependence in fresh water appears to be a more important regulatory mechanism than in the marine environment, variability in marine survival may be more important for determining the annual spawning run size given that density dependence in freshwater has the potential to buffer variability in survival in this environment.

The estimated carrying capacity for age-1 parr varied among populations by a factor of about 16 times. Grant and Kramer (1990) developed a relationship between body size and territory size for salmonids that they used to examine the hypothesis that territory size limits the maximum population density of salmonids. They concluded that body length explained 87% of the variation in territory size in juvenile salmonids despite variation in species. Here, factors other than body size (e.g. the environment, or number of territories with a habitat) must come into play to explain the differences in carrying capacity found among rivers.

The possibility that some of the among-population differences result from different sampling schemes for various rivers cannot be precluded. In some instances (e.g. the Stewiacke River) sites are selected using a stratified random method designed to sample habitat (using stream gradient as the habitat measure) in proportion to its availability. In others, sites are selected based on accessibility, and some habitat types are often not sampled due to confounding variables such as depth. However, for the most part, sites are sampled more or less consistently from one year to the next, so biases are likely to be consistent from year to year. If so, the resulting parameter estimates would be biased, however, the conclusions drawn about the timing and nature of density dependence should not be affected by these potential differences.

Meta-analysis has been touted as a way of improving biological and management parameters for fisheries (Myers and Mertz 1998b, Myers et al. 1999, Gibson and Myers 2004). However, our meta-analysis did not provide a plausible random effects distribution for the maximum survival rate from age-0-to-age-1. Given that α describes a stage-specific survival rate, rather than population growth rate (as in conventional SR models), the survival parameter has to range from zero to one in order to be biologically realistic. This allows the plausibility of the random effects distribution for survival to be evaluated. Such biological bounds are not known when estimating populations' maximum reproductive rates, and if similar estimation issues exist in those analyses, it is possible that they are only partially alleviated when these kinds of methods are applied. Note however, the model is only one part of the meta-analysis; the data standardizations allow for between population comparisons, and an examination of the effects of the priors (other data) on the resulting estimates for the individual populations.

When estimated using the mixed-effects model, habitat carrying capacity among rivers still varied by a factor of about 16. This variability is slightly less than that determined for alewife of about 25 times (Gibson and Myers 2003) and for Atlantic cod of more than 20 times (Myers et al. 2001), but is slightly higher than that determined for coho salmon of about 10 times (Barrowman et al. 2003). However, as discussed above, we cannot discount the possibility that some of this variability may result from differences in sampling design between some populations.

As outlined by Jonsson and Jonsson (2004), most salmon fisheries theory assumes that the mortality of salmon in the ocean is density-independent, a rationale based on the idea that the population density is far below the assumed carrying capacity for salmon in that

habitat. However, other density-dependent effects are possible, such as density-dependent predation on migrating smolt in estuaries or adults prior to upstream migration for spawning. Beverton's (1995) concentration hypothesis states that the potential for density dependence should be greatest when organisms are most concentrated, which is potentially during migration near the mouth of the river for salmon in the marine environment.

Given the data used in the analysis, the tests for density dependence in the marine environment would not distinguish between density-dependent survival and density-dependent age-at-maturity. Friedland and Hass (1996) examined the circuli spacing of 1SW and 2SW salmon within a smolt year class, and found that, in general, circuli spacings were wider for 1SW than for 2SW returns of the same smolt cohort. The 1SW fraction was correlated with late summer growth, suggesting that growth during this season is pivotal in determining the proportion of a smolt class that matures as a 1SW. If growth during that time period is density dependent, then age at maturity would also be density dependent.

Given the nature of anadromy, salmon populations are segregated from other salmon populations while in fresh water, but can mix with other populations while in the marine environment. In our analysis, density dependence in the marine environment was modeled using the abundance from the river specific population. This formulation is appropriate for testing whether density dependence is occurring while populations are segregated. Examples of potential density-dependent mechanisms that would be detected using this formulation are aggregative responses of predators during smolt migration or when adults are in the estuaries prior to migrating upstream. While populations are mixed at sea, the potential exists for density dependence to occur as a function of the total number of smolts emigrating from all rivers, although selection of an appropriate spatial scale for the analysis may be problematic. Myers et al. (1997) found the correlation scale for recruitment of pink and sockeye salmon was less than 300 km, suggesting widespread phenomena do not have a dominant influence for these species. Evaluation of this kind of relationship is a topic for future research.

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Table 1. Data time series used to investigate the timing and nature of density dependence in salmon populations in fresh water.

River	First year	Last year	Number of years with electrofishing data	Number of years with egg depositions	Mean number of electrofishing sites per year
Big Salmon River	1967	2002	20	23	4.65
Stewiacke River	1984	2001	17	0	33.76
Tobique River	1979	2004	22	16	15.68
Restigouche River	1972	2004	33	0	34.57
NW Miramichi River	1971	2004	34	13	18.85
SW Miramichi River	1971	2004	34	13	32.17
Margaree River	1991	2000	10	0	4.90
Nashwaak River	1981	2005	25	11	6.96
St. Mary's River	1985	2004	17	10	15.77

Table 2. Tests for density dependence in freshwater life stages for nine Atlantic salmon populations. Fits of linear models (density independent) are compared with the fits of Beverton-Holt models (density dependent: pure compensation) and Ricker (density dependent: overcompensation) models. Preferred models were selected using likelihood ratio tests at a 95% confidence level and the principle of parsimony: density independence was chosen unless the addition of a second parameter for density dependence provided a statistically better fit.

River	Stock	Recruit	Model	α	B or R_{asy}	σ	NLL	Model Choice
Big Salmon River	eggs	age0	Dens. independent	18.008		1.16	80.074	den-dep
	eggs	age0	Beverton-Holt	58.291	19.409	0.723	71.087	B-H
	eggs	age0	Ricker	27.357	0.247	0.862	74.431	
	age0	age1	Dens. independent	0.762		0.538	47.076	den-dep
	age0	age1	Beverton-Holt	1.404	18.643	0.411	42.761	
	age0	age1	Ricker	1.137	0.026	0.429	43.445	
	age1	age2	Dens. independent	0.36		1.014	30.854	den-ind
	age1	age2	Beverton-Holt	15.239	1.674	0.961	30.007	
	age1	age2	Ricker	0.536	0.046	0.993	30.518	
Margaree River	age0	age1	Dens. independent	0.452		0.143	31.137	den-ind
	age0	age1	Beverton-Holt	0.543	313.258	0.138	30.859	
	age0	age1	Ricker	0.548	0.002	0.138	30.832	
	age1	age2	Dens. independent	0.288		0.365	27.1	den-ind
	age1	age2	Beverton-Holt	0.913	19.353	0.313	25.712	
	age1	age2	Ricker	0.586	0.014	0.316	25.811	
NW Miramichi River	eggs	age0	Dens. independent	2.452		0.732	64.58	den-dep
	eggs	age0	Beverton-Holt	infinity	71.864	0.252	51.768	B-H
	eggs	age0	Ricker	6.794	0.027	0.321	54.679	
	age0	age1	Dens. independent	0.575		0.57	119.354	den-dep
	age0	age1	Beverton-Holt	0.965	37.398	0.47	112.952	
	age0	age1	Ricker	0.872	0.011	0.483	113.901	
	age1	age2	Dens. independent	0.31		0.566	73.549	den-dep
	age1	age2	Beverton-Holt	0.809	6.449	0.397	61.813	
	age1	age2	Ricker	0.572	0.037	0.415	63.306	

Table 2 (con't).

River	Stock	Recruit	Model	α	B or R_{asy}	σ	NLL	Model Choice
Nashwaak River	eggs	age0	Dens. independent	4.248		0.573	33.091	den-dep
	eggs	age0	Beverton-Holt	9.244	15.048	0.464	30.773	
	eggs	age0	Ricker	7.346	0.215	0.474	30.991	
	age0	age1	Dens. independent	0.436		0.684	68.608	dep-dep
	age0	age1	Beverton-Holt	1.709	8.381	0.344	52.08	B-H
	age0	age1	Ricker	0.831	0.033	0.411	56.401	
	age1	age2	Dens. independent	0.193		0.642	23.941	den-indep
	age1	age2	Beverton-Holt	0.382	1.81	0.596	22.151	
	age1	age2	Ricker	0.303	0.066	0.605	22.528	
Restigouche River	age0	age1	Dens. independent	0.318		0.425	89.988	den-dep
	age0	age1	Beverton-Holt	0.502	26.677	0.322	81.045	
	age0	age1	Ricker	0.457	0.009	0.331	81.94	
	age1	age2	Dens. independent	0.286		0.423	45.159	den-ind
	age1	age2	Beverton-Holt	0.279	45.069	0.422	45.039	
	age1	age2	Ricker	0.304	0.006	0.422	45.039	
SW Miramichi River	eggs	age0	Dens. independent	1.082		0.471	61.736	den-dep
	eggs	age0	Beverton-Holt	infinity	88.158	0.265	54.857	
	eggs	age0	Ricker	2.714	0.01	0.26	54.59	
	age0	age1	Dens. independent	0.294		0.413	104.239	den-ind
	age0	age1	Beverton-Holt	0.352	71.08	0.387	102.027	
	age0	age1	Ricker	0.374	0.004	0.385	101.92	
	age1	age2	Dens. independent	0.238		0.582	61.614	den-dep
	age1	age2	Beverton-Holt	0.65	4.245	0.354	45.157	
	age1	age2	Ricker	0.442	0.043	0.367	46.396	

Table 2 (con't).

River	Stock	Recruit	Model	α	B or R_{asy}	σ	NLL	Model Choice
St. Mary's River	eggs	age0	Dens. independent	3.93		0.737	29.45	den-ind
	eggs	age0	Beverton-Holt	5.315	22.258	0.697	28.94	
	eggs	age0	Ricker	5.367	0.094	0.706	29.065	
	age0	age1	Dens. independent	0.51		0.613	35.38	den-dep
	age0	age1	Beverton-Holt	1.267	6.817	0.406	29.185	
	age0	age1	Ricker	0.905	0.054	0.41	29.349	
	age1	age2	Dens. independent	0.18		0.429	4.757	den-ind
	age1	age2	Beverton-Holt	0.241	2.593	0.406	3.929	
	age1	age2	Ricker	0.261	0.074	0.402	3.785	
Stewiacke River	age0	age1	Dens. independent	1.065		0.528	43.017	den-ind
	age0	age1	Beverton-Holt	1.027	126.761	0.521	42.84	
	age0	age1	Ricker	1.172	0.007	0.521	42.834	
	age1	age2	Dens. independent	0.297		0.356	21.165	den-ind
	age1	age2	Beverton-Holt	0.344	19.47	0.334	20.186	
	age1	age2	Ricker	0.354	0.013	0.335	20.237	
Tobique River	eggs	age0	Dens. independent	1.992		0.592	41.226	den-ind
	eggs	age0	Beverton-Holt	2.516	36.058	0.537	39.955	
	eggs	age0	Ricker	2.805	0.048	0.533	39.859	
	age0	age1	Dens. independent	0.459		0.658	46.275	den-dep
	age0	age1	Beverton-Holt	2.228	6.317	0.361	35.452	B-H
	age0	age1	Ricker	0.714	0.03	0.484	40.752	
	age1	age2	Dens. independent	0.237		0.738	17.866	den-dep
	age1	age2	Beverton-Holt	infinity	0.885	0.606	14.318	
	age1	age2	Ricker	0.696	0.223	0.608	14.382	

Table 3. Comparison of the negative log-likelihoods obtained by fitting Beverton-Holt and Ricker models to juvenile salmon data for nine populations.

Life Stage Transition	River	Beverton-Holt	Ricker
egg-to-age-0	Big Salmon River	71.087	74.431
	Nashwaak River	30.773	30.991
	NW Miramichi River	51.768	54.679
	St. Mary's River	28.940	29.065
	SW Miramichi River	54.857	54.590
	Tobique River	39.955	39.859
egg-to-age-0 total		**277.381**	**283.615**
age-0-to-age-1	Big Salmon River	42.761	43.445
	Margaree River	30.859	30.832
	Nashwaak River	52.080	56.401
	NW Miramichi River	112.952	113.901
	Restigouche River	81.045	81.940
	St. Mary's River	29.185	29.349
	Stewiacke River	42.840	42.834
	SW Miramichi River	102.027	101.920
	Tobique River	35.452	40.752
age-0-to-age-1 total		**529.201**	**541.374**
age-1-to-age-2	Big Salmon River	30.007	30.518
	Margaree River	25.712	25.811
	Nashwaak River	22.151	22.528
	NW Miramichi River	61.813	63.306
	Restigouche River	45.039	45.039
	St. Mary's River	3.929	3.785
	Stewiacke River	20.186	20.237
	SW Miramichi River	45.157	46.396
	Tobique River	14.318	14.382
age-1-to-age-2 total		**268.312**	**272.002**

Table 4. Comparison of the estimates of the maximum survival rates between age-0 and age-1 (α) and the age-1 habitat carrying capacities (R_{asy}) obtained by fitting Beverton-Holt models to juvenile salmon densities. Models were fit to the data for each river both individually and simultaneously using a mixed-effects model.

	Individual Estimates		Mixed Effects Model Estimates	
River	α	R_{asy}	α	R_{asy}
Big Salmon River	1.40	18.64	1.19	21.87
Margaree River	0.54	313.26	0.84	115.47
NW Miramichi River	0.97	37.40	0.97	36.81
Nashwaak River	1.71	8.38	1.34	9.13
Restigouche River	0.50	26.68	0.53	24.90
SW Miramichi River	0.35	71.08	0.40	51.39
St. Mary's River	1.27	6.82	1.03	7.97
Stewiacke River	1.03	126.76	1.12	56.30
Tobique River	2.22	6.31	1.36	7.46

Table 5. Data time series used to investigate the timing and nature of density dependence in salmon populations in the marine environment.

River	First year	Last Year	Number of data points	
			1SW	2SW
Narraguagus	1995	2002	5	6
Nashwaak	1998	2003	6	5
LaHave	1996	2004	9	8
NW Miramichi	1999	2003	5	2
SW Miramichi	2001	2003	3	0
a la Barbe	1990	1993	4	4
St Jean	1989	2003	14	13
BecScie	1988	1995	8	8
de la Trinite	1984	2003	19	19
Highlands	1980	2000	10	9
Conne	1987	2004	18	0
Rocky	1990	2004	15	0
NETrepassey	1986	2004	19	0
Campbellton	1993	2004	12	0
WAB	1985	2004	20	0

Table 6. Tests for density dependence in the marine environment (smolt-to-1SW spawners) for fifteen Atlantic salmon populations. Fits of linear models (density-independent) are compared with the fits of Beverton-Holt models (density dependent: pure compensation) and Ricker (density dependent: overcompensation) models. The density-dependent model was selected when the addition of a second parameter for density dependence resulted in a statistically significant better fit (likelihood ratio tests at a 95% confidence level).

River	Model	α	B or R_{asy}	σ	NLL	Model Choice
Narraguagus	Dind	0.001		0.268	-18.765	den. ind.
Narraguagus	BH	0.001	inf	0.268	-18.765	
Narraguagus	Rick	0.001	0	0.268	-18.765	
Nashwaak	Dind	0.029		0.477	-1.309	den. ind.
Nashwaak	BH	0.217	0.467	0.371	-2.821	
Nashwaak	Rick	0.055	0.039	0.398	-2.398	
LaHave	Dind	0.024		0.497	-3.721	den. ind.
LaHave	BH	1.16E+10	0.322	0.406	-5.552	
LaHave	Rick	0.090	0.087	0.398	-5.714	
NW Miramichi	Dind	0.043		0.34	13.300	den. ind.
NW Miramichi	BH	0.049	63.563	0.337	13.254	
NW Miramichi	Rick	0.050	0.001	0.338	13.258	
SW Miramichi	Dind	0.054		0.268	10.006	den. ind.
SW Miramichi	BH	0.450	28.852	0.158	8.423	
SW Miramichi	Rick	0.145	0.002	0.142	8.099	
a la Barbe	Dind	0.004		0.375	-16.535	den. ind.
a la Barbe	BH	0.004	inf	0.375	-16.535	
a la Barbe	Rick	0.004	0	0.375	-16.535	
St Jean	Dind	0.004		0.242	-12.835	den. dep.
St Jean	BH	0.008	0.932	0.203	-15.328	
St Jean	Rick	0.007	0.004	0.206	-15.141	
BecScie	Dind	0.014		0.201	-21.199	den. ind.
BecScie	BH	0.013	inf	0.201	-21.199	
BecScie	Rick	0.014	0	0.201	-21.199	
de la Trinite	Dind	0.014		0.696	10.616	den. ind.
de la Trinite	BH	0.011	inf	0.696	10.616	
de la Trinite	Rick	0.014	0	0.696	10.616	
Highlands	Dind	0.015		0.576	-11.638	den. ind.
Highlands	BH	0.086	0.154	0.513	-12.779	
Highlands	Rick	0.037	0.087	0.51	-12.848	

Table 6 (con't.)

River	Model	α	B or Rasy	σ	NLL	Model Choice
Conne	Dind	0.047		0.458	31.573	den. ind.
Conne	BH	0.191	3.942	0.437	30.733	
Conne	Rick	0.112	0.012	0.434	30.608	
Rocky	Dind	0.033		0.172	-23.543	den. ind.
Rocky	BH	0.041	1.477	0.157	-24.957	
Rocky	Rick	0.041	0.022	0.156	-25.015	
NE Trepassey	Dind	0.055		0.350	-41.948	den. dep.
NE Trepassey	BH	1.098	0.08	0.230	-49.906	
NE Trepassey	Rick	0.153	0.692	0.235	-49.509	
Campbellton	Dind	0.067		0.332	15.266	den. dep.
Campbellton	BH	inf	2.6	0.232	10.953	
Campbellton	Rick	0.176	0.024	0.236	11.192	
WAB	Dind	0.059		0.500	8.909	den. ind.
WAB	BH	0.052	inf	0.500	8.909	
WAB	Rick	0.059	0	0.500	8.909	

Table 7. Tests for density dependence in the marine environment (smolt-to-2SW spawners) for nine Atlantic salmon populations. Fits of linear models (density-independent) are compared with the fits of Beverton-Holt models (density dependent: pure compensation) and Ricker (density dependent: overcompensation) models. The density-dependent model was selected when the addition of a second parameter for density dependence resulted in a statistically significant better fit (likelihood ratio tests at a 95% confidence level).

River	Model	α	B or Rasy	σ	NLL	Model Choice
Narraguagus	Dind	0.007		0.585	-19.789	den. ind.
Narraguagus	BH	0.006	inf	0.585	-19.789	
Narraguagus	Rick	0.007	0	0.585	-19.789	
Nashwaak	Dind	0.008		0.506	-6.714	den. ind.
Nashwaak	BH	0.007	inf	0.506	-6.714	
Nashwaak	Rick	0.008	0	0.506	-6.714	
LaHave	Dind	0.005		0.488	-16.446	den. ind.
LaHave	BH	inf	0.063	0.392	-18.190	
LaHave	Rick	0.022	0.104	0.384	-18.370	
NW Miramichi	Dind	0.009		0.303	1.879	den. ind.
NW Miramichi	BH	0.008	inf	0.303	1.879	
NW Miramichi	Rick	0.009	0	0.303	1.879	
a la Barbe	Dind	0.004		0.375	-16.535	den. ind.
a la Barbe	BH	0.004	inf	0.375	-16.535	
a la Barbe	Rick	0.004	0	0.375	-16.535	
St Jean	Dind	0.009		0.392	2.612	den. ind.
St Jean	BH	0.010	4.787	0.388	2.486	
St Jean	Rick	0.011	0.002	0.388	2.480	
BecScie	Dind	0.009		0.531	-17.314	den. ind.
BecScie	BH	inf	0.052	0.479	-18.14	
BecScie	Rick	0.025	0.154	0.488	-17.991	
de la Trinite	Dind	0.010		0.771	5.568	den. ind.
de la Trinite	BH	0.007	inf	0.771	5.568	
de la Trinite	Rick	0.010	0	0.771	5.568	
Highlands	Dind	0.010		0.401	-16.743	den. ind.
Highlands	BH	0.033	0.132	0.336	-18.333	
Highlands	Rick	0.024	0.087	0.321	-18.750	

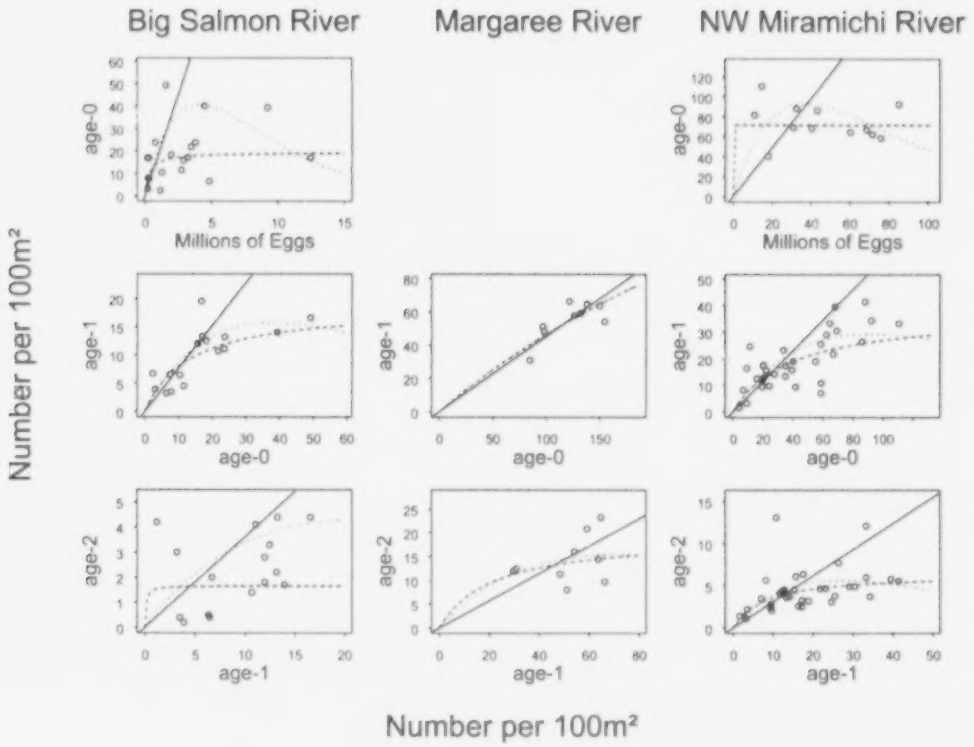

Figure 1. Observed (points) and predicted (lines) densities of Atlantic salmon obtained by fitting three models to the data. The data are the observed abundance or density within a cohort by age. The solid line is a one-parameter model that shows the fit obtained based on the assumption that survival is density independent. The dashed and dotted lines show the fits obtained from two-parameter Beverton-Holt and Ricker models respectively. The former model assumes that survival is purely compensatory, whereas the later model allows for overcompensation. Parameter estimates and statistical comparisons of the fits are provided in Table 2.

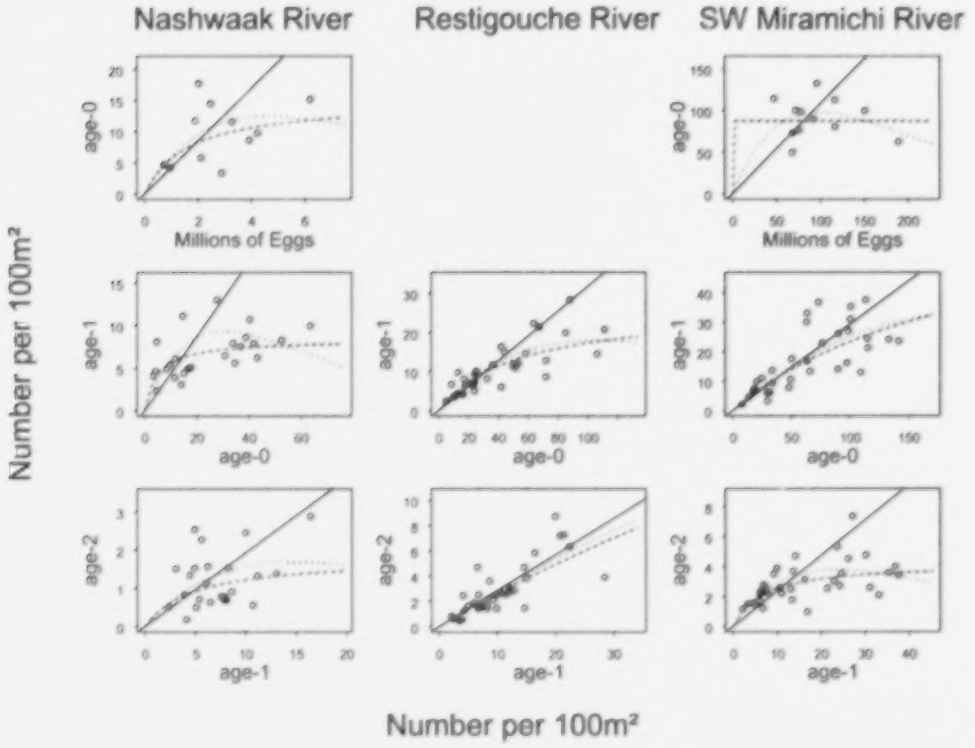

Figure 1 (con't).

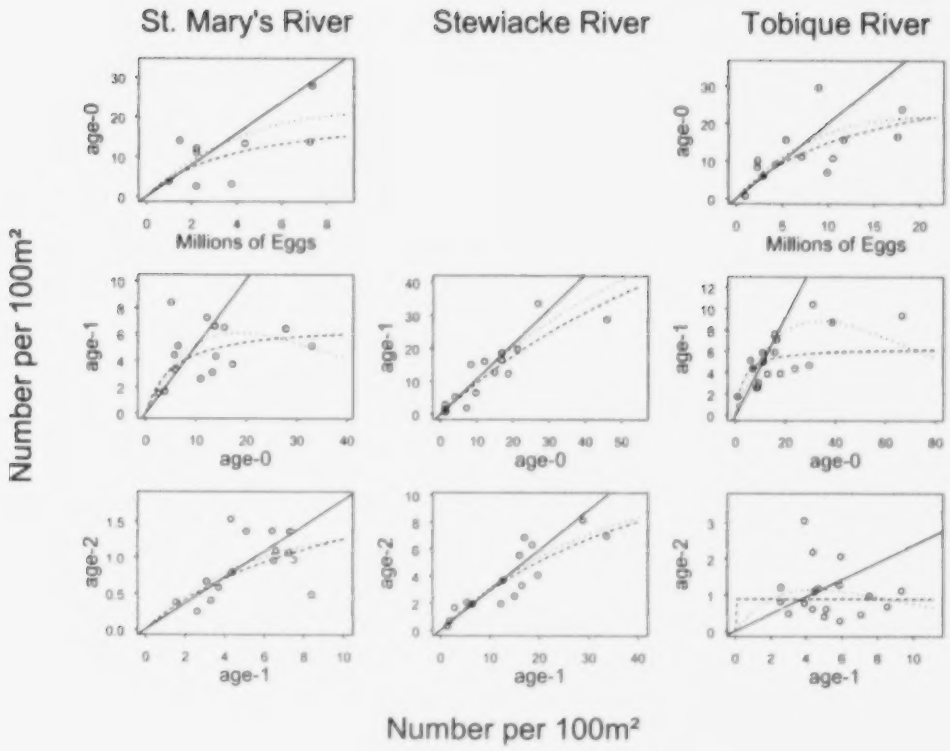

Figure 1 (con't).

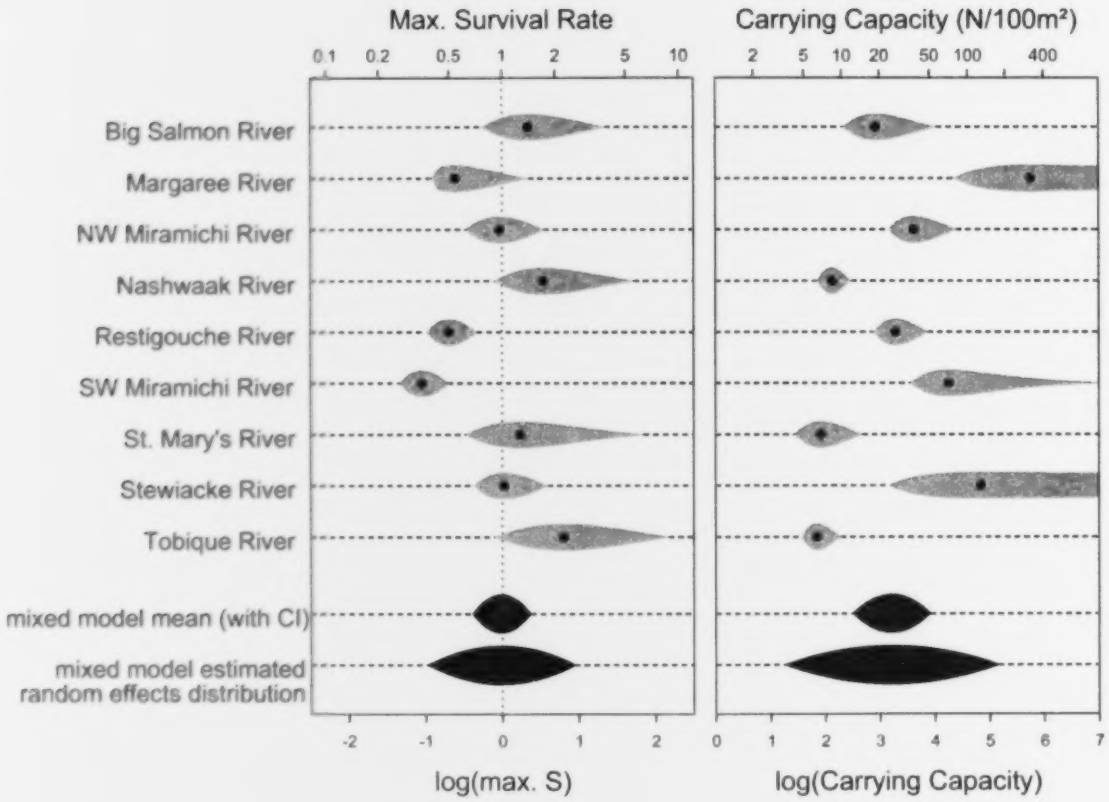

Figure 2. A meta-analytic summary of the maximium age-0-to-age-1 survival rate and the habitat carrying capacity for age-1 parr for nine salmon populations. The light grey shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence interval. The height of the profile is used to gauge the relative plausibility of different values (greater height is more plausible). The black dot is the maximum likelihood estimate for each parameter. The dark grey shaded regions show summaries of the mixed model results. The "mixed model mean" represents the estimated mean of the logarithm of each parameter with a 95% confidence interval. The "mixed model estimated random effects distribution" is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed-effects model.

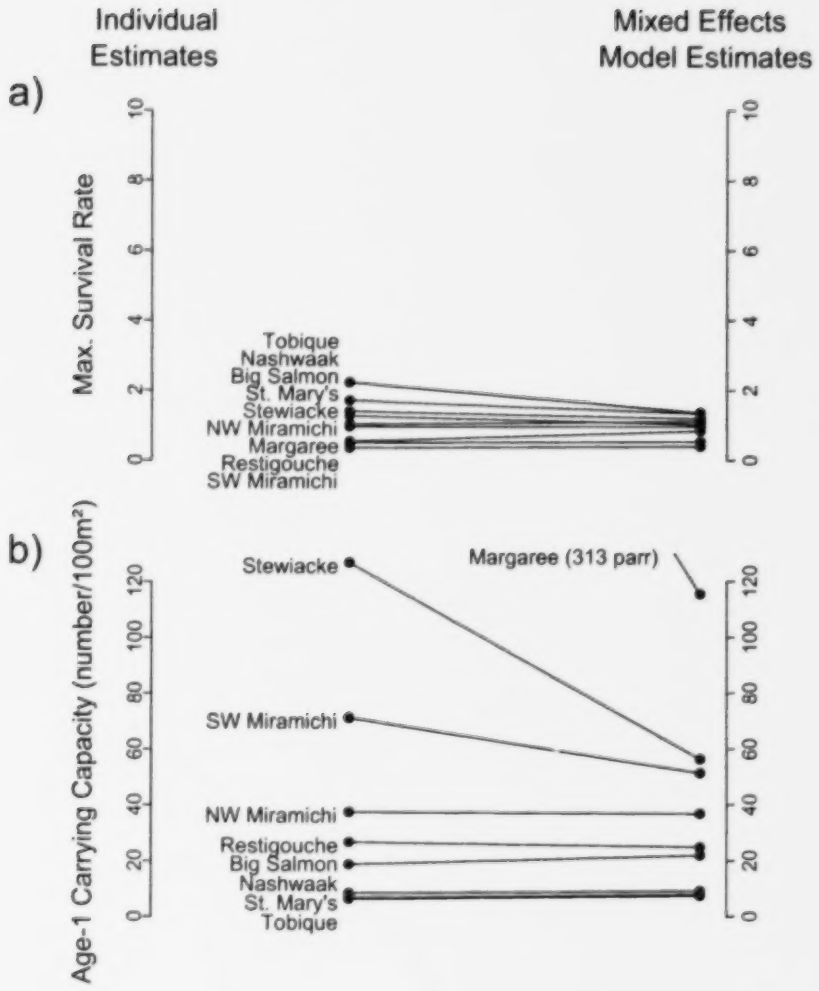

Figure 3. A comparison of the estimates of the maximum age-0-to-age-1 survival and the habitat carrying capacity for age-1 parr obtained from individual regressions on each salmon population and the empirical Bayes estimates obtained from the mixed model.

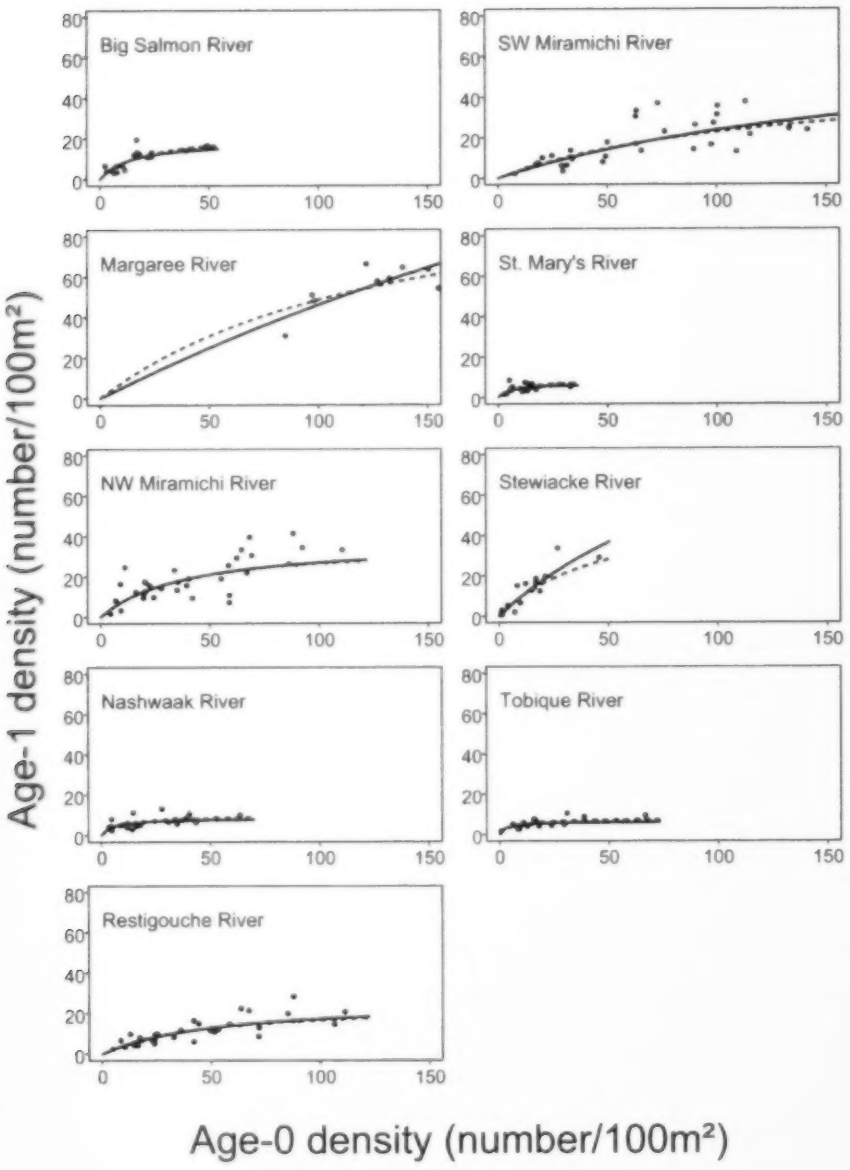

Figure 4. Beverton-Holt models fit to age-0 and age-1 densities for nine salmon populations. The solid line is the spawner-recruit relationship obtained for each population individually and the dashed line is the spawner-recruit relationship for each stock from the mixed-effects model.

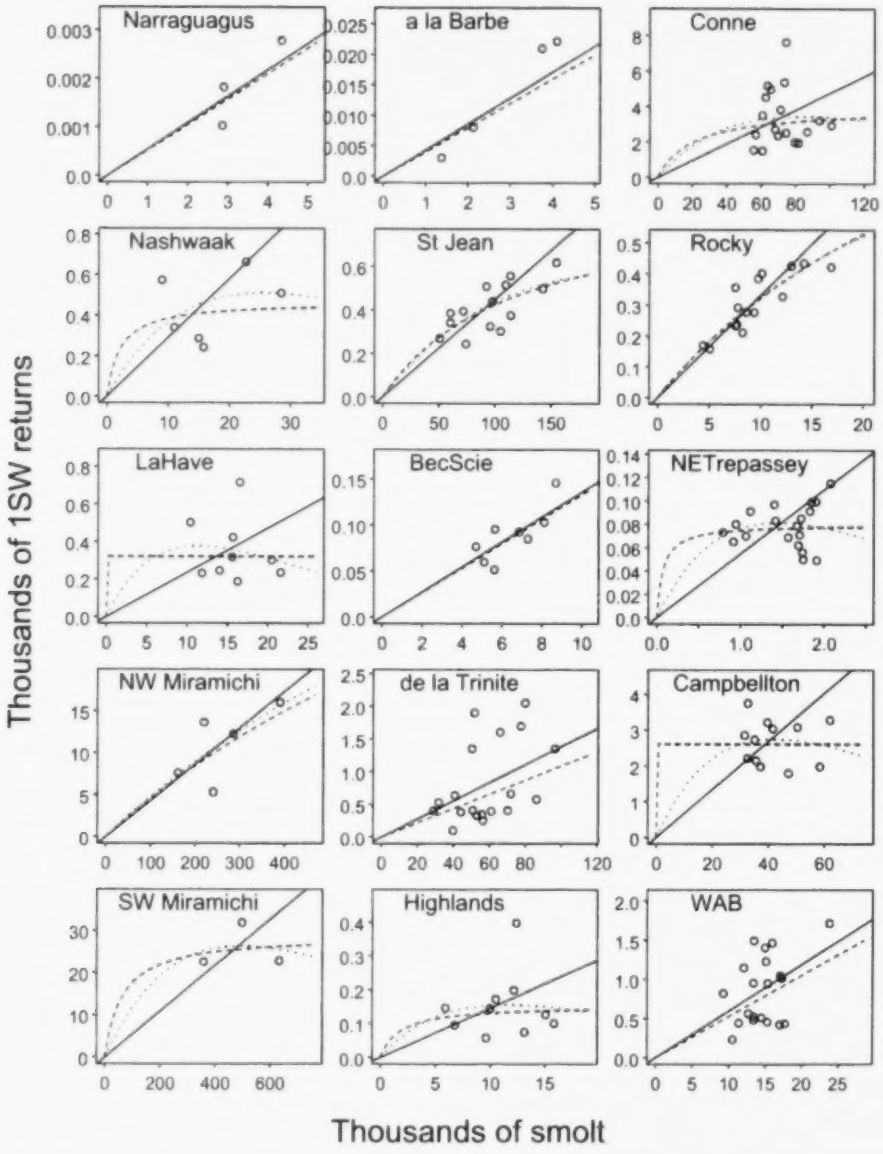

Figure 5. Observed (points) and predicted (lines) densities of Atlantic salmon obtained by fitting three models to the smolt-to-1SW spawner data. The data are the observed abundance or density within a cohort by age. The solid line is a one-parameter model that shows the fit obtained based on the assumption that survival is density independent. The dashed and dotted lines show the fits obtained from two-parameter Beverton-Holt and Ricker models respectively. Parameter estimates and statistical comparisons of the fits are provided in Table 6.

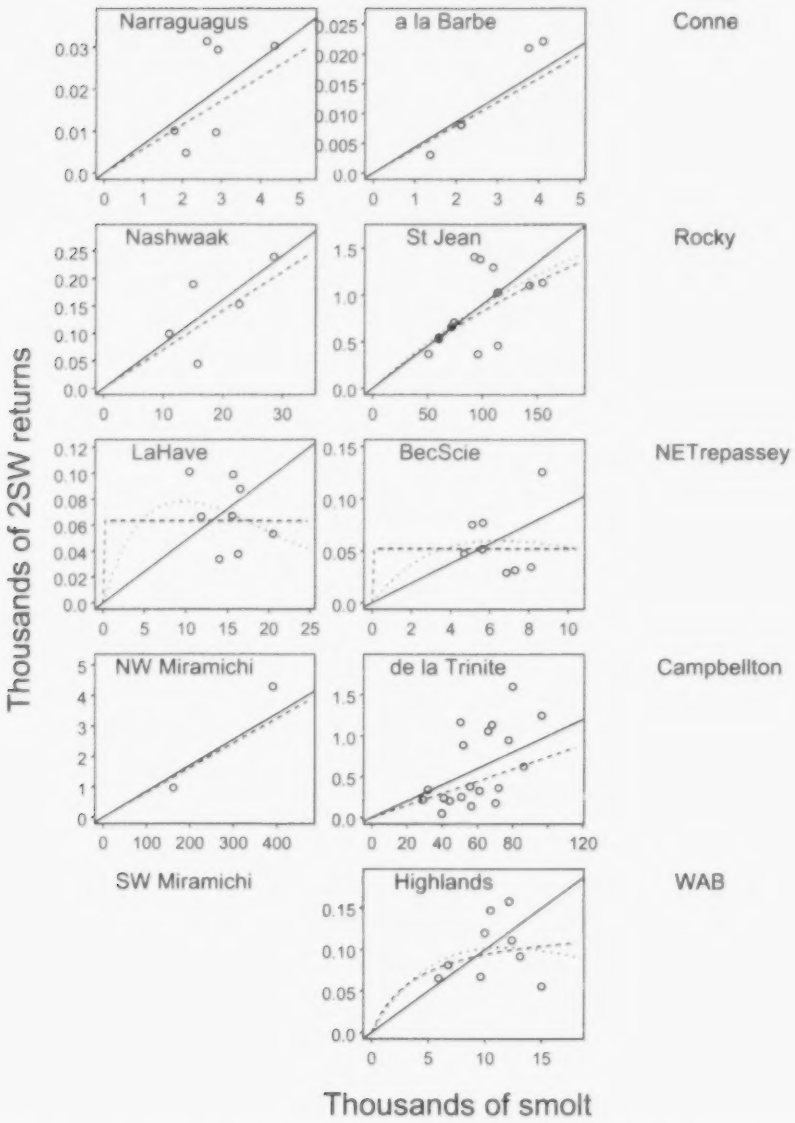

Figure 6. Observed (points) and predicted (lines) densities of Atlantic salmon obtained by fitting three models to the smolt-to-2SW spawner data. The data are the observed abundance or density within a cohort by age. The solid line is a one-parameter model that shows the fit obtained based on the assumption that survival is density independent. The dashed and dotted lines show the fits obtained from two-parameter Beverton-Holt and Ricker models respectively. Parameter estimates and statistical comparisons of the fits are provided in Table 7.